

# Utilization of Pheromones in the Population Management of Moth Pests

by R. T. Cardé\*

Pheromones are substances emitted by one individual of a species and eliciting a specific response in a second individual of the same species. In moths (Lepidoptera) generally females lure males for mating by emission of a sex attractant pheromone comprised of either one or more components. Since 1966 the identification of the pheromone blends of many moth pests has allowed investigations into the use of these messengers for population manipulation. Pheromone-baited traps may be used both to detect pest presence and to estimate population density, so that conventional control tactics can be employed only as required and timed precisely for maximum effectiveness. Attractant traps also can be utilized for direct population suppression when the traps are deployed at a density effective in reducing mating success sufficiently to achieve control. A third use pattern of pheromones and related compounds is disruption of pheromone communication via atmospheric permeation with synthetic disruptants. The behavioral modifications involved in disruption of communication may include habituation of the normal response sequence (alteration of the pheromone response threshold) and "confusion" (inability of the organism to perceive and orient to the naturally emitted lure). Disruption of communication employing the natural pheromone components as the disruptant has been most successful, although nonattractant behavioral modifiers structurally similar to the pheromone components also may prove useful. Possible future resistance to direct pheromone manipulation may be expected to involve the evolution of behavioral and sensory changes that minimize the informational overlap between the natural pheromone system and the pheromone control technique.

## Historical Perspective

Since at least the 18th century naturalists have been aware that males of many insects could discover the females at considerable distances, even when the females were placed in concealment. Upon this principle of "sembling," London aurelians took females of day-flying moths "in a box with a gauze lid into the vicinity of the woods, where, if the weather be favourable, she never fails to attract a numerous train of males, whose only business appears to be an incessant, rapid undulating flight in search of the females. One of these is no sooner descried, than they become so much enamoured of their fair kinswoman, as absolutely to lose all fear for their own personal safety" (1).

It was thought then that the males' discovery of a female was "through the medium of the sense of smell" (1), a mechanism demonstrated con-

clusively by Fabre in the mid-19th century (2). In spite of these early studies, the field of chemically mediated behavior in insects did not acquire much additional sophistication until the mid-20th century. In 1959 Karlson, Butenandt and Lüscher (3,4) coined the term "pheromone" to refer to substances emitted by one individual and eliciting a specific reaction in a second individual of the same species. Two years later (5) Butenandt and his colleagues culminated a 30 year effort by identifying *trans*-10, *cis*-12-hexadecadien-1-ol as the female-produced sex attractant of the commercial silkworm, *Bombyx mori*, the first pheromone to be deciphered. These two events and an increased awareness of the environmental and health effects of conventional pesticides (6) gave impetus and funding to alternative methods of pest control. Thus, most research programs directed toward elucidation of the chemical identity and behavioral role of pheromones usually have been concerned with the economically injurious species in the expectation that the synthetic pheromone could be

\*Department of Entomology, Pesticide Research Center, Michigan State University, East Lansing, Michigan 48824.

used in a pest management system. Ten years ago the expectations clearly were that pheromones would become part of a new third generation of pesticides. Pheromones would not only be efficacious but environmentally safe and rather target specific as well. Upon close examination of these goals in 1975 it is glaringly evident that they have been achieved so far on only a limited basis.

Initially, pheromone manipulation can be considered only where relevant behavioral responses to chemicals exist. For the most part, in insect pests the phenomenon of chemical cues for bringing the sexes together for mating has been a prime focus of applied uses of pheromones. Regrettably, however, many insects do not use pheromones for long-distance mate finding, often relying instead on visual or acoustical cues. Hence, pheromone manipulation of certain pests is not likely.

Secondly, many of the insect pheromone identifications of the 1960's and even today either have proved to be either incorrect in their structural assignments or they have actually described only a portion of the pheromone blend, so that the biological activity of the synthetic chemicals has not been sufficient to manipulate the pest's behavior in the field. And lastly, once the pheromone has been described—correctly or not, completely or not—often large-scale demonstrations of efficacy have been attempted immediately, usually on the futile assumptions that little need be understood of the pest's behavior since it would be eradicated presently and that the intricacies of formulation are outside the province of the pheromone field.

In insects, the chemistry of pheromones (7) and the diverse behavioral patterns mediated by pheromones (8) have been the subject of excellent recent reviews. This paper will discuss findings and theory as applicable to the utilization of pheromones in integrated pest management systems with particular emphasis on the lepidopterous (moth) species, one of the insect orders about which much is known of pheromone chemistry.

## Pheromones in Monitoring Systems

The first and the most obvious use of pheromones has been in detection and survey of insect pests. In principle, the utilization of a synthetic pheromone-baited trap for monitoring the presence and abundance of an economically important species does not differ from the early naturalists' use of female-baited traps for collecting. Indeed, pheromone gland extracts were used for monitor-

ing the spread of the gypsy moth (*Porthetria dispar*) some 50 years ago (9), much as the synthetic pheromone disparlure (*cis*-7,8-epoxy-2-methyloctadecane) is used currently (10). In current integrated pest management programs, however, precise knowledge of the presence and abundance of a pest species may allow "on-line" decisions as to the control tactics. Ideally, conventional pesticides would be employed only when the pest population was of sufficient density to cause economically defined damage. The timing of a pesticide application could be directed either toward the most vulnerable life stage or in biological "windows" when the pesticide would least affect the manipulation of other pests and beneficial species.

Synthetic pheromone monitoring of the summer fruit tortrix moth (*Adoxophyes orana*), a prominent pest of apples in the Netherlands, has resulted in a marked change in the application of conventional insecticides, previously determined by calendar dates (11). In this species the maximum benefit is derived when the insecticide is applied a few days after egg hatch, just as the larvae are dispersing to their feeding sites, prior to their construction of a protected spun leaf. This susceptibility window can be predicted accurately with the use of sticky traps baited with the synthetic of the natural pheromone, a 9:1 admixture of *cis*-11 and *cis*-9-tetradecenyl acetates (12,13). Thus, in the Netherlands, the widespread use of pheromone monitoring traps for this species has resulted in the use of fewer insecticide applications with more control effectiveness (11).

In Michigan a similar program is being implemented by Croft and his colleagues for monitoring the codling moth, *Laspeyresia pomonella*, on apples. Traps baited with *trans*-8, *trans*-10-dodecadien-1-ol, the sex pheromone (14), give a biological fix on the seasonal profile of moth emergence, and this information in conjunction with thermal accumulation units can be used to time a conventional insecticide application to the susceptibility window that occurs after egg hatch and prior to larval entry into the fruit (15). In an attempt to refine the model upon which such on-line management decisions will be based, future utilization will involve correction for environment conditions that can affect trap catch. For example, in Michigan, temperatures below 13–14°C (H. Riedl, personal communication) eliminate male codling moth attraction and hence trap catch, although these conditions generally do not directly influence overall population trends. Similarly, trap catch is not directly proportional to the moth population, since in dense situations competition with virgin females lowers trap efficiency (16). Notwithstanding, even a

simple empirical approach of relating trap catch to damage may allow a reduction in conventional applications. In South Africa, Myburgh et al. (17) have demonstrated that the codling moth population is potentially injurious only when the pheromone trap catch rises either above 10 males per hectare during any one of the three annual generations or above two males per hectare per week in the midsummer and late summer broods.

Similar empirical experiences with the codling moth on apples in British Columbia have shown that a pheromone trap catch of two or more males per hectare per week is the critical value indicating the necessity of a conventional pesticide. In six orchards, one orchard did not require any sprays by this criterion over the 2-yr study period. Overall the mean number of sprays in the six orchards for all pests declined from eight prior to the test's initiation to 5.6 and 3.1 in the first and second study years, respectively, without an increase in insect or mite damage to either fruit or foliage (18).

In New York, where the insect pest complex on apples is more formidable, an experimental pest management program has included pheromone monitoring traps for six potential tortricid moth pests. The average number of sprays in the study region between petal fall and harvest has been reduced from seven or eight to four or five while maintaining pest-free fruit (J. Tette, personal communication).

Although many additional pest management programs utilizing a pheromone-baited monitoring device could be given, the principle involved is directly analogous to the preceding cases: each involves the utilization of a naturally-occurring chemical communication system, usually at vanishingly low rates. Whereas a conventional pesticide might be applied at roughly  $10^3$  g/ha, the amount of pheromone requisite for one monitoring trap could be only  $10^{-4}$  to  $10^{-7}$  g/ha. Once volatilized from a pheromone dispenser into the atmosphere, the pheromone would be indistinguishable from naturally secreted pheromone, less in quantity than that emitted from a high level of natural infestation and present in such miniscule quantities as to be virtually undetectable by currently available instrumentation. No adverse health or environmental consequences seem to be indicated. Because of these considerations, the ready degradability of nearly all pheromone compounds, and the salient fact (from a regulatory viewpoint) that pheromone monitoring is neither designed nor claimed to effect control, the United States Environmental Protection Agency does not require registration of pheromones for this use pattern.

## Pheromone Trapping for Population Suppression

Perhaps the earliest effort to employ a pheromone communication system for control was the innovative but unsuccessful use of female-baited traps by Kirkland (19) in 1893 to suppress *P. dispar*, the gypsy moth, in Massachusetts. The principle involved is not far removed from surveillance with pheromone monitoring traps, but instead of capturing only a proportion adequate for estimation of population density, in mass trapping the proportion of the population captured must be sufficient to reduce successful mating appreciably and thereby effect control.

Curiously, pheromone trapping for control currently is regulated in the United States in exactly the same manner as are conventional insecticides. Extensive toxicological tests as well as a demonstration of efficacy are a prerequisite to registration. Depending on the species used for comparison, the quantity of pheromone volatilized in a monitoring situation for one species could exceed that employed for mass trapping control of another pest, since the most effective pheromone dispenser dosages vary with species. In any mass trapping use pattern the amount evaporated could be miniscule, and often less than might be emitted per unit area from a high natural infestation.

A variety of theoretical considerations will determine the success of the strategy. In moths, the key parameters concern the density of organisms, the ratio of traps to organisms, the relative attractiveness of the traps and of the organisms, and the degree of the pest's endemism in the control area.

An understanding of the complex interactions of these parameters may help to specify the number of traps necessary for successful suppression. To effect a population reduction in most moth species the techniques may allow perhaps 0 to 5 or 10% of the females to mate. Obvious features determining the likelihood of a male being captured by a trap versus locating a "calling" mate include the ratios between both traps and calling females to the available males. Adult emergence of the sexes is rarely synchronous, and for most species the males precede the females (protandry). For any given spatial deployment of traps in the early stage of the adult flight season, the ratio of traps to females will be greater than this ratio toward the end of the flight period. The percentage of a given number of females mating will increase with the density of males, even though the trap catch also will be elevated.

Mating in almost all Lepidoptera occurs during discrete daily intervals (20). In the moth species

that have been investigated the proximate environmental cues setting the rhythms of male responsiveness and female calling include sunrise (lights-on), sunset (lights-off) and a decrease in ambient temperature (20,21). In many species the diel rhythms of male and female sexual activity are somewhat asynchronous, with male responsiveness occurring prior to female attractiveness (22). As pointed out previously (23,24), such a timing dichotomy will favor males being trapped over locating females, since the traps emit the pheromone continuously. Depending on the timing difference, the number of traps required for suppression may be lowered appreciably from the density necessary if the rhythms were coincident.

In certain species the diel response interval of the male (and not the female's periodicity of pheromone emission) seems to determine the time of attraction. *P. dispar* males in the United States are attracted to females and synthetic pheromone during the same daily interval, indicating that in this species the male rhythm determines the time of attraction (23). In mass trapping for control of *P. dispar*, pheromone traps would have no diel timing advantage.

Other strategy considerations are the pheromone trap's effective drawing range and efficiency of trap capture. Pheromone dispensers can be designed to emit pheromone at higher rates than from the calling organism, thereby creating an increase in the pheromone's active space (25), the volume of atmosphere containing a concentration of pheromone above the threshold required to elicit positive upwind orientation. Thus, an artificial dispenser has the potential to lure males from a greater distance than the effective range of a calling female. However, such an artificially high rate of pheromone emission may not increase trap catch, since in some species optimum close range orientation seems to be related to a discrete emission rate, with higher and lower values lowering the trap catch (26-28).

Intrinsically nonattractive pheromone components also may mediate orientation close to the pheromone dispenser, increasing trap catch two- to tenfold (28,29). The trap design (e.g., configuration, color, stickiness) may be of crucial importance to catch effectiveness. Curiously, there is a paucity of simple observational studies which describe absolute trap efficacy: how many individuals arriving in the vicinity of a trap are actually ensnared (30).

Other important parameters include the pattern of adult survivorship; the frequency of multiple

matings (although in most moth species with multiple matings the preponderance of oviposition is the result of the first mating); and possible "competition" effects (the suggestion that absolute trap attractiveness is related to the density of females) as seems to be the case in dense adult populations of *L. pomonella* (16). Theoretical considerations of pheromone trapping systems using some of the previously discussed parameters can be found in Roelofs et al. (31) for *A. velutinana* and Beroza and Knipling (10) for *P. dispar*.

In the Lepidoptera there are few case histories of successful mass trapping for control using damage as the criterion of efficacy. In New York apple orchards a density of 1 pheromone trap per mature, standard apple tree (100 traps/ha) produced commercially acceptable control (2.3-0.1% fruit injury) of *A. velutinana* in two orchards of 18 and 11 ha in a 3-yr test. It was found that at this trap density a sparse pest population at the initiation of trapping was required, for the same technique was unable to prevent population increases when attempted on moderate infestations (31,32). In New York grape vineyards, pheromone trapping produced a similar effect with *A. velutinana* and with another tortricid, the grape berry moth (*Paralobesia viteana*), although in this test the control achieved was slightly less than the commercially acceptable level (33). Since *A. velutinana* feeds on numerous hosts and is widely distributed outside orchards and vineyards (34), gravid females may immigrate into the mass trapping area. Effective control for such non-endemic pests may necessitate a buffer trapping zone at the periphery of the crop.

Attempts to trap in New York apple orchards at reduced trap densities (35) of from 9 to 37 traps/ha for the entire tortricid pest complex (*A. velutinana*, *Choristoneura rosacena*, *Grapholitha prunivora*, *G. molesta*, *Pandemis limitata*, and *L. pomonella*) have not been successful from a fruit damage standpoint. However, for most of these species the attractiveness of the pheromone bait compared to a virgin female is unknown. Improvements in traps, pheromone dispenser, or the identification of additional secondary pheromone components may yet allow effective orchard mass trapping at a density of less than 100 traps/ha. In regions where a single lepidopterous pest is the primary concern, as is the case with *L. pomonella* in the western United States, control by pheromone trapping should be both technically and economically feasible.

## Disruption of Pheromone Communication by Atmospheric Permeation

In 1967 the utilization of pheromones as a direct control agent was postulated from the preliminary field trials of Gaston and Shorey (36) with *Tricoplusia ni*, the cabbage looper moth. In their pioneering experiments the synthetic sex attractant pheromone, *cis*-7-dodecenyl acetate (37), was emitted from 2.5 cm planchets deployed 1 m above the ground in a 10 × 10 array with a 3 m spacing between evaporator stations. The resultant atmospheric concentration of synthetic pheromone was sufficient to eliminate the feral males' location of female-baited traps, whereas in the experimental check plots the females lured over 100 *T. ni* males.

This pattern of pheromone application currently is termed disruption of communication (instead of "confusion") to avoid inference as to the as yet unresolved mechanism that effects a change in orientation behavior. The disruptant modification may be due to "confusion," in which the responding organism is less capable of correctly perceiving and thus locating the natural pheromone emitters in an atmosphere permeated with synthetic pheromone. Alternatively, the omnipresence of synthetic pheromone could elevate the organism's threshold of pheromone response, i.e., the lowest atmospheric concentration of pheromone at which a behavioral response occurs. This latter hypothesis of a qualitative behavioral change has received support from a variety of laboratory behavioral bioassays.

Traynier (38) demonstrated in *Anagasta kuhniella*, the Mediterranean flour moth, that the rate and incidence of habituation was not critically dependent upon the dosage of pheromone, provided that the concentration of the habituating treatment was above that required for responsiveness. In other words, under the test protocol, habituation in *A. kuhniella* appeared to be an all or nothing phenomenon. It should be pointed out that these early *A. kuhniella* tests were confounded by the use of crude female extracts as the stimulus. Crude extracts often contain either nonpheromone compound or component ratios that may either reduce or eliminate the response (39–43). The pheromone system of *A. kuhniella* does appear to consist of a single compound (44). In contrast to *A. kuhniella*, Sower et al. (45) reported in laboratory experiments with *Sitotroga cerealella*, the Angoumois grain moth, that the level of habituation achieved was related both to the intensity of the chemical stimulus and to the treatment's duration.

Gradations of response modification dependent upon the concentration and duration of the treatment may be more applicable to field-use situations where the atmospheric concentration of the synthetic pheromone disruptant may be lower than the concentration of natural pheromone in close proximity to the emitter. In other words, when the natural pheromone or a mimic is used as a disruptant, its atmospheric concentration in a field use situation may be insufficient to elicit a full repertoire of behavioral response, e.g., an entire sequence of upwind flight, landing, close-range orientation, precopulatory behavior, and copulatory attempts. Nevertheless, the disruptant's atmospheric concentration would be efficacious in raising the organism's response thresholds for the behavioral events at the beginning of the sequence, and hence reducing the chances for successful location of a mate.

In some species the complete abolition of pheromone responsiveness may necessitate disruptant dose levels that are economically impractical for field situations. However, it is possible that full elimination of mating response is not a prerequisite to successful population suppression. In *Argyrotaenia velutinana*, the redbanded leafroller moth, a microencapsulated spray of two of its pheromone components (29), *cis*-11- and *trans*-11-tetradecenyl acetates (89:11), in an apple orchard effectively suppressed the ability of males to locate pheromone sources, but this same treatment was ineffective in eliminating ability of males to mate with females in very close proximity (confined to small cages) (46). Thus, the above case illustrates disruption of no more than the initial stages of the mating sequence, long-range orientation, and possibly landing, rather than complete habituation of pheromone responsiveness.

Perhaps much of the difficulty in determining the behavioral modifications involved in disruption of pheromone communication rests upon our rudimentary perceptions of moth mating behavior. That the majority of moth (and other insect) pheromone systems are based on two or more natural components was not established until after 1971, so perhaps it is not unexpected that the precise behavioral role of the individual components has been elucidated in but one species, *Grapholitha molesta*, the oriental fruit moth. This tortricid pest utilizes *cis*-8-dodecenyl acetate (47) with ca. 7% *trans*-8-dodecenyl acetate (48,49) as a blend mediating long-range upwind orientation, whereas close-range orientation, landing, wing fanning, hairpencil display, and copulatory attempts can be elicited by the simultaneous emission of a third

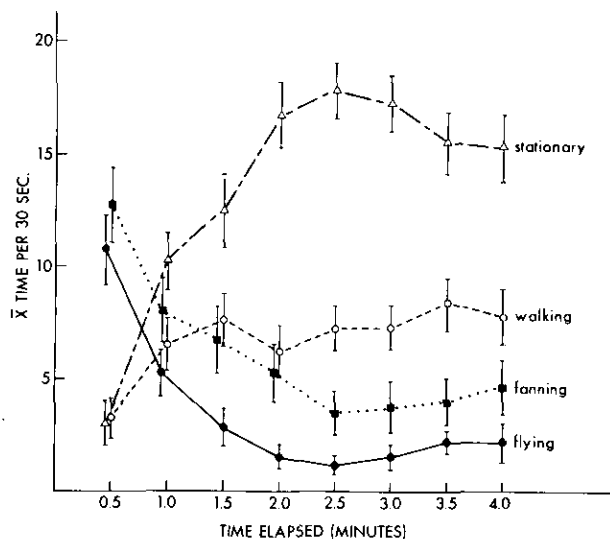


FIGURE 1. Behavioral responses of wild *Grapholitha molesta* (Oriental fruit moth) males during confinement in the first 4 minutes after attraction in the field to 100  $\mu$ g *cis*-8-dodecenyl acetate (8% *trans*) and 300  $\mu$ g dodecyl alcohol on a rubber septum dispenser. During the 4 min of observation the initial frequencies of both flying (including hovering) and wing fanning decrease, while the incidences of both walking and quiescence increase.

component, dodecyl alcohol (28,30). The habituating effect of these three components presented simultaneously are given in Figure 1.

Disruption of communication of *G. molesta* might be based either upon modification of long-range orientation employing *cis*-8- and *trans*-8-dodecenyl acetate (92:8) as a disruptant, or upon modification of the precopulatory mating responses using either dodecyl alcohol or *cis*-8-dodecanol (another compound is also apparently effecting close range behavior) as the disruptant. Perhaps some combination of the two tactics might be utilized. Obviously a more intimate understanding of the factors mediating attraction and mating can reveal new disruption strategies.

The mode of action of a wide variety of non-pheromone chemicals that negatively influence attraction, along with their potential for disruption, are other poorly understood aspects of insect orientation. Such modifiers of behavior have been variously termed "inhibitors," "maskers," and "anti-attractants." These mechanistic terms unfortunately connote behavioral and neurophysiological processes that may be inapplicable to their actual role in manipulation of the attraction process. Metarchon, the term coined by Wright (50) to denote behavioral modifiers, or simply "behavioral modifiers" may be of more heuristic value.

The presence in the pheromone-producing gland of a naturally-occurring substance that reduced attractiveness when emitted from the same locus as

the attractant was demonstrated (39) in *Porthetria dispar*, the gypsy moth, and later shown to be 2-methyl-*cis*-7-octadecene (40), the supposed natural precursor to the pheromone, *cis*-7,8-epoxy-2-methyloctadecane (51). It was suggested (40) that the structural similarities between the attractant epoxide pheromone and the olefin precursor indicated that both compounds might interact at the same antennal receptor sites, as in the multiple compound interactions previously proposed for odor quality coding in *Argyrotaenia velutinana* (26,52-54). However, single-cell studies by O'Connell showed that two structurally similar pheromone components in the *A. velutinana* pheromone, *cis*-11- and *trans*-11-tetradecenyl acetates, interacted with at least two different functionally independent receptor sites on each of two odor-sensitive sensory neurons in each sensillum trichodeum of male *A. velutinana* antennae. In addition, the two sensory neurons displayed characteristic differences in spike amplitude (53) and in some of the temporal aspects of impulse generation "such as response latency, interspike interval distribution, and duration of response" (54).

Likewise, in male *P. dispar* the olefin and epoxide each could evoke distinctive types of impulses and patterns of spike activity, with the appropriate behavioral response being determined via a more central integrative process. Another possibility would be the olefin acting to affect negatively the receptor sites' ability to generate slow potentials in response to the epoxide by interfering with a common pheromone binding site. A third explanation would be the perception of these compounds by two different sensory neurons each with its own functionally independent receptor sites. Impulse generation by either neuron would result in a particular behavioral response encoded in its own "labelled line."

In *P. dispar* the pheromone, related epoxides and the olefin have been reported to fire the same olfactory cells, with the olefin not eliciting inhibitory responses. Independent cells selectively responsive either to the pheromone or the olefin were not detected (55). The reduction in attractiveness elicited by the olefin when emitted simultaneously with the pheromone thus appears inconsistent with a labeled line mechanism utilizing more than one "line." However, in another behavioral context, atmospheric permeation with the olefin, the olefin evoked an increase in male searching behavior (56), consistent with labeled line encoding or at minimum, the hypothesis of functionally independent receptor sites existing on the antenna. There is no evidence for the presence of the olefin in the natural effluvium from female *P. dispar* (40).

The *raison d'être* for the reduction in attractiveness effected by the olefin may be analogous to the so-called "inhibitors" of the attractants of a number of other lepidopterous species. In *Laspeyresia pomonella*, the codling moth, the female-produced pheromone is *trans*-8,*trans*-10-dodecadien-1-ol (14), and marked reductions in attractiveness of this pheromone are effected by the concomitant emanation of a variety of pheromone analogs: the pheromone's three geometrical isomers (the *cis,cis*, the *cis,trans*, and the *trans,cis*) (57); the acetate of the pheromone (58); monounsaturated analogs such as *cis*-8-dodecen-1-ol (59), and several other ether derivatives (60). None of these compounds (whose behavioral effects were revealed by empirical field screening) appear to be part of the natural communication system. The nonparsimonious explanation would be that each "inhibitory" compound was perceived by a labeled line sensor cued to negating the attraction response sequence. The simplest mode of action involves the inhibitory compounds evoking a pattern of spike activity distinguishable at the central nervous system level from the pheromone response.

In contrast to the reductions in trap catch effected by nonpheromones as exemplified by *P. dispar* and *L. pomonella*, in many species a similar diminution in trap catch can be achieved by the alteration of the naturally emitted ratio of the pheromone components. The attractant pheromone in *A. velutinana* is comprised of *cis*- and *trans*-11-tetradecenyl and dodecyl acetates (9:1:15) (29). Trap catch is reduced as the proportion of *trans*-11-tetradecenyl acetate in the blend is elevated, so that the *trans* component can be considered inhibitory to attractancy at certain ratios. Laboratory bioassays established that an excess of the *trans* component suppresses a variety of behavioral responses including activation and flight (61). In the Lepidoptera analogous situations exist for a number of multicomponent attractant systems: incorrect ratios lower attractiveness (62-64). In *A. velutinana* the single cell antennal responses indicate that the *cis* and *trans* isomers are evidently perceived via independent sensors, since each isomer elicits a maximal response in two independent cell types. The exact encoding program (other than it cannot be labeled line) is not yet apparent, however, for the *trans* isomer does fire the cell that is maximally responsive to *cis*, and the converse also holds true (54).

Labeled line sensors for inhibitory compounds have been implicated in some Lepidoptera. Laboratory assays of *Plodia interpunctella*, the Indian meal moth, and *Cadra cautella*, the almond moth, have revealed that nonpheromone com-

pounds that diminish the responses of the males of these species apparently do not affect the input of the pheromone sensors, since males can be experimentally habituated to the inhibitors while remaining responsive to their pheromones (65).

The foregoing exemplars suggest that behavioral modifiers of attractancy may act through a variety of sensory input codings. Behavioral modifiers have been proposed for use in the disruption technique since these compounds seemingly have the virtue of interfering with the attraction process. In the preceding situations, the context of presentation of the modifier was simultaneous emission from the same locus as the attractant. In techniques where the modifier is dispersed over large areas, the resultant effect on orientation can be quite different.

In *P. dispar* the olefin attraction suppressant could elicit male searching behavior when dispersed in an atmospheric permeation technique from spaced evaporator stations (56). In other field trials with a microencapsulated formulation, the olefin appeared much less effective than the epoxide pheromone in disrupting attraction (66), although, it should be added, the comparative emission characteristics of the active ingredients were not assessed, so that it is uncertain what the actual dose levels in the atmosphere were. Similarly, in *G. molesta*, dodecyl acetate was noted to depress trap catches when emitted with the attractant (67,68), whereas release of dodecyl acetate from evaporator devices *elevated* the catch of nearby traps (68). In *T. ni* the emanation of *cis*-7-dodecen-1-ol with the pheromone (69), *cis*-7-dodecenyl acetate (37), eliminates the males' attraction sequence, with measurable suppression evident at 0.1% of the alcohol relative to the acetate. Notwithstanding, the alcohol is far less effective as a disruptant than the pheromone when used in an atmospheric permeation technique (70).

To date most of the successful field tests of disruption have employed the pheromones rather than behavioral modifiers as disruptants, although modifiers may yet be demonstrated to be useful for manipulation of communication.

## Disruption of Communication with Point Source Dispensers

The early investigations dispensed the pheromone (or closely analogous compounds) from evaporation stations deployed on a fixed spatial arrangement. The objective was to evaporate the disruptant at a given rate per unit area rather than to achieve a uniform and complete dispersion of disruptant. Evaluation of efficacy protocols generally

involved comparison of the catch of either synthetic pheromone-baited or organism-baited traps in both the treated and comparable check areas. Significant disruption (catches in the experimental areas reduced by more than 95%) was demonstrated by Shorey, Gaston and co-workers in a number of moths, most notably *T. ni* and *Pectinophora gossypiella* (the pink bollworm) with the sex pheromone (71) and *cis*-7-hexadecenyl acetate (a pheromone mimic) (72), respectively.

The use of spaced evaporator devices was also effective on two tortricid moth pests of grape in New York. Female-baited and pheromone-baited trap catches were reduced more than 95% and crop damage was suppressed to near economically-acceptable levels (33). Additionally, this technique has been evaluated on small plots (generally ca. less than 0.02 ha) with a number of other moth species for suppression of trap catch.

Recently this spaced-release station method has been tried on a large scale in the Coachella Valley of California using the true pheromone of *P. gossypiella*, a 1:1 admixture of *cis*-7, *cis*-11 and *cis*-7, *trans*-11-hexadecadienyl acetates. The pheromone was evaporated into a 2500-ha field of cotton for 20 weeks, reducing the numbers of pink bollworm infesting cotton bolls up to 75% at less of an expense than involved in a conventional pesticide program (73).

Associated with this type of pheromone delivery system may be technical and economic difficulties in maintenance of the release stations. Possibly more important, however, is that spaced emission devices may allow layers and fenestellae of disruptant-free air. The use of a sprayable, microdispersible formulation should eliminate unevenness in atmospheric permeation and allow application with the same techniques as followed for conventional pesticides.

## Disruption of Communication with Microdispersible Formulations

The earliest encouraging tests with a sprayable slow release matrix were conducted with *P. dispar*, the gypsy moth and a microencapsulated formulation of its sex attractant (74–76). Most of these field trials used moderate dose levels (e.g., ca. 20 g pheromone/ha) aerially sprayed onto the forest canopy. The actual evenness of application throughout the various canopy levels was difficult to evaluate and the emission characteristics (percent and rate of active ingredient volatilization) from the slow release matrix have not been stated.

Efficacy of mating disruption for most trials as judged from mating in either very sparse or artificial populations appeared adequate to assume good potential for population reduction. A test (77) utilizing the same formulation sprayed in 1-ha plots from the ground (yielding good coverage up to 10–15 m into the canopy, below which most mating occurs) suggested excellent mating disruption success, even in comparatively dense adult populations, and reported qualitative modifications of the males searching behavior. With an increased knowledge of formulation emission properties and of the effect on mating behavior, the prospects for population manipulation of this important defoliator of eastern United States hardwood forests are excellent.

Similar success (46,78) has been demonstrated with *A. velutinana* and a microencapsulated formulation of two of its three pheromone components: *cis*- and *trans*-11-tetradecenyl acetates (89:11). Applied at 22 g pheromone/ha, this treatment can suppress synthetic pheromone baited-trap catch 98–99%. Since synthetic-baited traps are severalfold as attractive as virgin female-baited traps, it is reasonable to suppose that the treatment would effectively suppress the males' ability to locate females. Despite the efficacy of this release matrix, its emission properties, as measured in the laboratory, are far from ideal. Total release of the pheromone amounted to less than 4%, with nearly all volatilization occurring in the first few days (46). Thus in these tests the actual release of active ingredient was less than 1 g/ha per application.

As noted previously, alterations of the natural pheromone ratio of 11-tetradecenyl acetates reduces trap catch. Thus it was of interest to determine the comparative disruptive effect of both 50:50 *cis:trans* and pure *trans* formulations. In a test in New York vineyards, the 89:11, 50:50 and 0:100 formulations produced 98, 89 and 67% reductions, respectively, in trap catch (78). In *A. velutinana*, as perhaps in other moths, the most effective disruptant appears to be the natural ratio of pheromone components.

## Evolution of Resistance to Pheromone Manipulation

Past experience has demonstrated convincingly that the usage of conventional pesticides selects for the evolution of resistant biotypes, although there are notable examples of the use of petroleum oils as pesticides for over 50 yr without changes in efficacy. When the pheromone use pattern involves



traps for population monitoring, it is improbable that the selective pressure will be of sufficient magnitude to produce a resistant biotype, i.e., to effect a change in the communication system. But in some cases the widespread and long term use of pheromones as control agents eventually may be anticipated to spawn populations oblivious to this manipulation.

Mass trapping for control would be an intense selective pressure. In species utilizing a blend of pheromone components, the use of the "natural" medley in traps could select for individuals emitting an altered blend ratio and responders favoring the new mixture. In attempting to design a control strategy, knowledge of secondary pheromone chemicals affecting subtle aspects of mating behavior would be of prime importance. Failure to duplicate the organism's natural chemical message completely could bare a ready target: the chemical missing in the synthetic bait only need become an obligatory blend component necessary to full behavioral response. This evolutionary change would not involve either new pheromone blend components or ratios, nor would it necessitate new pheromone sensors and encoding pathways.

For species that employ but a single pheromone component, the evolutionary task could be arduous as it would likely necessitate evolution of both new chemical sensors and encoding procedures responsive to the new secondary compounds that confer specificity. Possibly entirely novel pheromone components also will be required, unless other previously unimportant emanations could fulfill this role. Development of resistance in species using a single pheromone component requires concomitant evolution of a novel responder and emitter communication system and should be less likely than in species with a pheromone blend in which resistance may only involve modification of an existing responder system.

In addition to changes in the pheromone communication system, selection by mass trapping might facilitate other alterations in behavior. Diel and seasonal temporal synchrony among the pheromone responders and emitters would be favored, since both precocious daily response and early emergence (generally protandry) would tend to increase capture while decreasing mating success. Individuals achieving the closest coincidence of times of responsiveness to female receptivity would be most apt to mate successfully. (Evolution of such timing changes would in turn alter the ratio of traps to insects necessary for control.) Also favored would be the accentuation of differences between the rate of pheromone volitalization from the synthetic pheromone dispenser and from the

natural organisms. Rate of emission is a factor demonstrated to be of great importance in obtaining optimum trap catch in some species (26,27). Increased emphasis on either visual (79) or, rarely, auditory (80) orientation cues might become a selective advantage.

Disruption of communication also can be viewed as a considerable selective pressure. Discussion of the potential mechanisms of resistance to disruption of communication techniques is clouded by the lack of understanding of exactly how disruption of communication is accomplished. If control is achieved largely via confusion (as defined previously) rather than habituation, then evolution of resistance may proceed through alterations minimizing the informational overlap between the disruptant and the pheromone system. Thus, when the disruptant is a blend of components identical to the natural pheromone, selection may favor blend modifications that allow the natural emitters to differ from the disruptant. Field trials with the tortricid *A. velutinana*, as noted, demonstrated that the natural 89:11 *cis:trans* ratio of 11-tetradecenyl acetates was more effective as an attraction disruptant than either the 50:50 or the 0:100 formulations (78). Hence, continued utilization of the 89:11 blend might favor a blend ratio change in *A. velutinana*.

Similarly, disruptant mixtures comprised of only part of the natural pheromone medley may select for resistance involving an increased emphasis on the component missing from the disruptant. This pathway would not be available to species that utilize a single pheromone compound. In such organisms, resistance might involve a new pheromone component, much as suggested in the mass trapping hypothesis.

If disruption is accomplished via habituation at the central nervous system level (with, for example, the precision and success of orientation remaining intact in brief exposures to the disruption treatments), selection simply may favor responders that are less readily habituated.

Nonpheromone chemicals used as disruptants may interact with the same sensor as the pheromone, and in this situation evolution of resistance could involve either an antennal binding site change allowing more accurate discrimination between the disruptant and the pheromone or a change allowing more accurate discrimination of the sensory input into central nervous system. In organisms possessing labeled line sensors coded to compounds that terminate the pheromone response sequence, the resistance might involve the abolition of this "inhibitory" behavioral response, by functional elimination either of the "line" or the sensor.

A key factor in the likelihood of rapid change in pheromone communication systems will be the amount of genetically determined natural variation in the responders and the emitters. To date this question has only been investigated in responders of *G. molesta*, the Oriental fruit moth. Males are attracted by a range of component blend ratios with the optimum attractant isomer ratio being ca. 7% *trans*-8 in *cis*-8-dodecenyl acetate. Lessened attractiveness of both 3% and 11% *trans* blends could be due either to a broad sensory tuning, in which males respond to a variety of ratios, or to disparate phenotypes with different response modalities. In *G. molesta* the field trials using a capture-mark-recapture technique with wild males showed no detectable phenotypic variation (81).

## Conclusions

In attempting to summarize both the current role of pheromones in insect pest management and the prospects for future utilization, a multiplicity of behavioral patterns that are under pheromone regulation and an ever-expanding diversity of identified pheromone structures must be considered. Notwithstanding, in pest species possessing a relevant behavioral response—such as attraction to a chemical emitter—and following correct characterization of the pheromone's chemistry, the potential of population manipulation is considerable.

The use of pheromone-baited traps for precise monitoring of a pest density is underway in Eurasia, Australia, South Africa, and the Americas. This population information allows conventional pesticides to be applied only as required and at times that exert maximum effect. Future applications of pheromone-based monitoring systems seem widespread, since this use pattern will not require the lengthy and costly registration procedures necessary for economic poisons.

Utilization of pheromones for direct population control is clearly a future prospect. In the case of mass trapping the technique has been demonstrated feasible and efficacious for certain species but so far this method has remained economically impractical for the particular organisms tested, for control could be achieved at lower cost using a conventional insecticide. Since pheromones are natural products they generally will be considered nonpatentable; without proprietary rights, who will bear the not inconsiderable costs of toxicological studies and registration?

Disruption of communication with pheromones or related compounds poses analogous obstacles. There is increasing evidence that a sprayable

microdispersable formulation of disruptant is highly effective, even in the suboptimal formulations currently available. But to reduce the application rate of active ingredient to reasonably economical dosages and to allow season-long tests of efficacy based on damage criteria, formulation matrices that volatilize much of the active ingredient at a relatively constant rate must be developed. Although a release matrix may have clear proprietary rights, the pheromone may not, so that the impetus for development and registration is lacking.

By the nature of their function—transmission of an unambiguous message—pheromones are target-specific. If pheromones continue to be classed as economic poisons, the development of pheromones for control will be hindered; the cost of registration for a single pest will rarely be justifiable commercially. Given the general chemical lability, nontoxicity (82), and very low rate of application of pheromones as a class, it is not evident why pheromones should be regulated in exactly the same manner as the poisons it is hoped pheromones would supplant.

The second correct attractant pheromone structure was reported only ten years ago (37). Remarkable progress in identification techniques and instrumentation has occurred in the interim, and currently dozens of pheromones are characterized each year. It is now possible for a pheromone monitoring system to effect an appreciable change in a conventional pesticide schedule within a year or two after the pheromone's elucidation. During the next ten years perhaps we can look forward to the development and implementation of pheromones as direct control agents.

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